A PRELIMINARY REVIEW OF COLOMBIAN ANTS (HYMENOPTERA: FORMICIDAE) PRESERVED IN COPAL[1]

Mark B. DuBois[2, 3, 4], John S. LaPolla[5]

ABSTRACT: Ants preserved in copal are reported from localities in Colombia, South America. Representatives of 21 genera (5 subfamilies) are reported from Boyaca Department; representatives of 24 genera (6 subfamilies) are reported from Santander Department. Comparisons between the faunas were made using presence / absence measures and alpha diversity measures. Of the genera encountered in Santander Department, a significant number were typically terrestrial foragers rather than arboreal foragers. It is theorized that the majority of resin trapped specimens were foraging at or near the soil surface. Of the genera encountered in Boyaca Department, a high percentage was typically arboreal foragers. It is theorized that resins trapped these specimens as they foraged well above the soil surface. Comparisons were also made to the fossil ants found in amber from the Dominican Republic and to the extant ant fauna of Colombia. The ants preserved in copal are more similar to those found in amber from the Dominican Republic than to those presently known from Colombia. It is theorized that this is due to the method of collection (resin trapped specimens) which may exclude a large number of genera.

Although ants dominate many terrestrial ecosystems, they are relatively uncommon as fossils and sub-fossils. Many ant wing fragments are represented in shales (from Eocene to more recent deposits). Specimens typically represent reproductives which flew over a body of water and were drowned and buried in volcanic ash or mud (Carpenter, 1930). Worker ants are typically encountered as fossils preserved in hardened plant resins (amber and copal). The former have been extensively studied (for example, Wheeler, 1915 reviewed the ant fauna of the Baltic amber; Wilson, 1985 reviewed the ant fauna of the Dominican Republic amber). Many new species (and some new genera) have been described from amber (for example, Baroni-Urbani, 1980a described the first Attini and Baroni-Urbani, 1980b described the first Odontomachini; Ward, 1992 described new species of *Pseudomyrmex*).

Poinar (1996) indicated that resin is the viscous stage (sticky and pliable) when it emerges from plants. After the resin dries and can not be molded (pressure results in fractures instead of an impression), the material is called copal. The change from resin to copal varies but can be as short as a month. Within copal the molecules have started to polymerize (however, the surface can be-

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[2] 116 Burton Street, Washington, IL 61571-2509.

[3] Research Affiliate, Center for Biodiversity, Illinois Natural History Survey, 607 East Peabody Drive, Champaign, IL 61820.

[4] Send Reprint requests to the Washington, Illinois address (of MBD).

[5] Department of Entomology, Rutgers University, New Brunswick, New Jersey 08901.

come sticky when copal is subjected to organic solvents). Copal is softer than amber and melts at lower temperatures. The material continues to polymerize over time. When the melting point is between 200 and 380 degrees Celsius, the hardness is between 2 and 3 (Mohs scale), and the surface does not become sticky when subjected to organic solvents, the material is called amber. Poinar (1996) estimated the time for copal to become amber probably takes between 2 and 4 million years.

Specimens preserved in copal have been relatively overlooked. Exceptions include Schluter and Von Gnielinski, 1987 and DuBois, 1998. Part of the reason for this neglect is that the species and genera represented in copal all appear to be modern forms. Most copal is thought to be of Recent, Pleistocene, or Pliocene origin (Poinar, 1992). Analyses using C_{14} methods on Colombian copal yielded age ranges from 10 to 500 years old (one sample was between 380 and 500 years old, another 210 and 310 years old, and a third between 10 and 80 years old) (Poinar, 1996). A number of arguments supporting both Recent and Tertiary ages for this material were presented by Stinchcomb (1998). Regardless of the age, we believe that this material is worthy of further study. It can provide a link (historically) with older material and can shed light on the ant fauna of a region prior to intensive human activities. Such material may also be used to document distributional changes of genera and species within an ecosystem. The purpose of this paper is to quantify some of the ant biodiversity contained in copal from two departments in Colombia (Boyaca and Santander).

METHODS AND MATERIALS

Ant specimens preserved in copal were directly examined and identified with a Wild dissecting stereomicroscope. Specimens were identified to genus using Bolton, 1994 and Hölldobler and Wilson, 1990, and directly compared with recent specimens in the collection of the senior author. Many specimens were oriented in such a manner that identification to species was difficult without significant re-cutting and re-polishing of the matrix. Tools were not readily available for this work, thus specimens were grouped into morphospecies. All analyses were then done at the generic level. All data was included in a presence / absence matrix (by genus) and was analyzed using the Biodiv program version 4.1 (Baev and Penev, 1993). Jaccard's coefficient (weighted for species richness) was selected to quantify biodiversity. With presence / absence data, additional comparisons were made with the known extant Colombian ant fauna and with the ant fauna reported from amber of the Dominican Republic.

Quantitative analyses were also conducted for comparisons between the two sites. As with presence / absence data, the Biodiv program formed the basis for this analysis. A suite of indices was selected since calculation of different indices causes some loss of information (Magurran, 1988). The selected suite

follows that used by DuBois (1995): Margalef Index, Reciprocal of Simpson's Index, Shannon Diversity Index, Q Statistic, Berger-Parker Dominance Index, Alpha Diversity Index and Pielou Evenness Index. Since comparisons were made at the level of genus, some information regarding species diversity was undoubtedly lost. However, a number of genera were represented by a single morpho-species (sometimes a single specimen).

GEOLOGICAL DETAILS

Specimens were obtained from Allan Graffham (Ardmore, Oklahoma). Duplicate material has been returned to him. All material originated from localities in Colombia: Boyaca or Santander Departments. Schlee (1984) attributed the Santander locality to the vicinity of "Peña Blanca." It is presumed this locality is within Santander Department. Santander and Boyaca are adjacent departments in the Colombian Andes. Poinar and Poinar (1994: 187) indicated these localities are probably near the Magdalena River (which forms the western boundary of parts of Boyaca and Santander Departments). Poinar (1996) indicated the bulk of this material "...comes from the Departments of Santander, Boyaca, and Bolivar; more specifically, near the cities or villages of Bucaramanga, Giron, Bonda, Medellin, Peñablanca, Mariquita, and Valle de Jesus." It should be noted that Medellin is in Dept. Antioquia. Although the actual localities have not been personally examined, the general habitus of the amber deposits is a layer (containing copal) covered by a layer of volcanic ash. Initial discovery of copal deposits is along road cuts. Depth of the copal bearing layer ranges between 1 and 3 meters beneath the soil surface (in Santander) and up to 10 meters beneath the soil surface (in Boyaca). Efforts are presently underway to obtain a sample of this ash so its age can be determined (Allen Graffham, pers. comm.). Copal is presumed to be of Recent, Pleistocene, or Pliocene age. Since it floats, it can readily be re-deposited. Landslides may also re-deposit this material. Therefore, ages of copal are difficult to determine. Carbon$_{14}$ analysis has yielded dates ranging from mid-1700's through mid-1900's. However, the oils used to polish the material (and subsequent heat generated during polishing) may significantly alter the matrix and may not allow for proper carbon$_{14}$ dating. Ken Anderson (pers. comm.) indicated this material is of "resins of undetermined geological age, but probably not of great antiquity." Poinar (1992) indicated that all known Colombian material is of Pleistocene age. However, Poinar (1996) indicated that the majority appears less than 500 years old. Until the age of the overlying volcanic ash is determined and more samples are subjected to modern dating techniques, we refer to the age of this material as undetermined, but probably Recent.

It appears that this material originated from resins of *Hymenaea* (Leguminosae: Caesalpinaceae) or similar plants (Poinar, 1992; Poinar and Poinar, 1994; Poinar, 1996). Details regarding the origin and deposition of this

material are sketchy. Poinar (1996) indicated this resin comes from the Algarroba tree (*Hymenaea courbaril*, *H. oblongifolia*, and *H. parvifolia*) which is "...widely distributed throughout Southern Mexico, Central America, The Antilles, and the northern regions of South America." He indicated the resin accumulates between the bark and wood and under the roots.

BIOLOGICAL DETAILS

A total of 329 ant specimens (318 workers, 5 gynes, and 6 males) from Colombian copal were contained in 163 individual pieces of copal. Representatives of most species are stored in the personal collection of M. DuBois (Washington, Illinois). All material identified to genus is listed in the appendix. Specimens belong to the subfamilies listed below. Percentages for Boyaca and Santander represent only those specimens obtained from that locality. Although the bulk of specimens are Dolichoderinae (and most of these are *Azteca*), there is a significant amount of diversity. However, there are significant differences in biodiversity between these two sites.

	Total Specimens Examined	Percent of Total Specimens	Percent of Boyaca Specimens	Percent of Santander Specimens
Dolichoderinae	169	51.37%	65.80%	17.35%
Ecitoninae	4	1.22%	0.00%	4.08%
Formicinae	27	8.21%	6.49%	12.24%
Myrmicinae	93	28.27%	19.05%	50.00%
Ponerinae	13	3.95%	3.03%	6.12%
Pseudomyrmicinae	23	6.99%	5.63%	10.20%

Of the subfamilies represented, the majority of specimens are distributed among the following genera. As before, the percentages for Boyaca and Santander represent only those specimens collected at that locality.

	Total Specimens Examined	Percent of Total Specimens	Percent of Boyaca Specimens	Percent of Santander Specimens
Azteca	130	39.51%	55.84%	1.02%
Camponotus	22	6.69%	4.76%	11.22%
Crematogaster	47	14.29%	9.52%	25.51%
Dolichoderus	23	6.99%	6.49%	8.16%
Pheidole	22	6.69%	5.19%	10.20%
Pseudomyrmex	23	6.99%	5.63%	10.20%

Eight of the genera are represented by single specimens (*Acromyrmex*, *Atta*, *Gnamptogenys*, *Myrmecina*, Unidentified Myrmicinae, *Proceratium*, *Rogeria*, and *Smithistruma*).

COMPARISONS

For comparisons to be made with other faunas, we restricted our analyses to the level of genus. We anticipated a significant difference between species given the distributions (over time and geography); however, many genera represented are ubiquitous throughout the New World tropics. We anticipated limited variation in genera due to this fact coupled with the sampling method (sticky plant resin). Thus, a number of arboreal and above ground foraging genera should be typically represented.

Similarity Measures (Presence / Absence Data)

Comparisons were made with several disparate ant assemblages. Material presented in copal from both Boyaca and Santander Departments was compared to determine differences in the composition of the two fossil assemblages. The known extant ant fauna of Colombia was also compared (at the level of genus) to determine similarities between recent and fossil ants from Colombia. Finally, the known ant fauna found in amber from the Dominican Republic was also compared. This latter material is significantly older and geographically removed from Colombia. We included it as a baseline since many genera found in Colombia are presently known throughout northern South America and the Caribbean. Similarity might also indicate the relationship to method of preservation as well as possibly shedding additional light on the age of the copal.

The following sources of genera were used: Colombian copal (material directly examined from Boyaca and Santander), modern ant fauna of Colombia (Kempf, 1972 and Fernández et al., 1996), and Dominican Republic amber (Wilson, 1985). In all cases, names of genera were updated using Bolton, 1995.

Calculation of Jaccard's coefficient resulted in the following values: Boyaca vs. Santander (0.57), Colombian copal vs. Dominican Republic amber (0.44), all fossils vs. extant Colombian ant fauna (0.21) (Fig. 1). A value of 1 would indicate complete similarity and 0 would indicate complete dissimilarity. Although the faunas preserved in copal from Boyaca and Santander are somewhat similar, they exhibit significant differences (represented by the coefficient of 0.57).

Examples of the differences noted above include the genus *Azteca* that is represented mostly by specimens from Boyaca. Additionally, fossils of some genera (*Neivamyrmex*, *Smithistruma* and *Strumigenys*) are known exclusively from Santander while other genera (*Acromyrmex* and *Cephalotes*) are known exclusively from Boyaca.

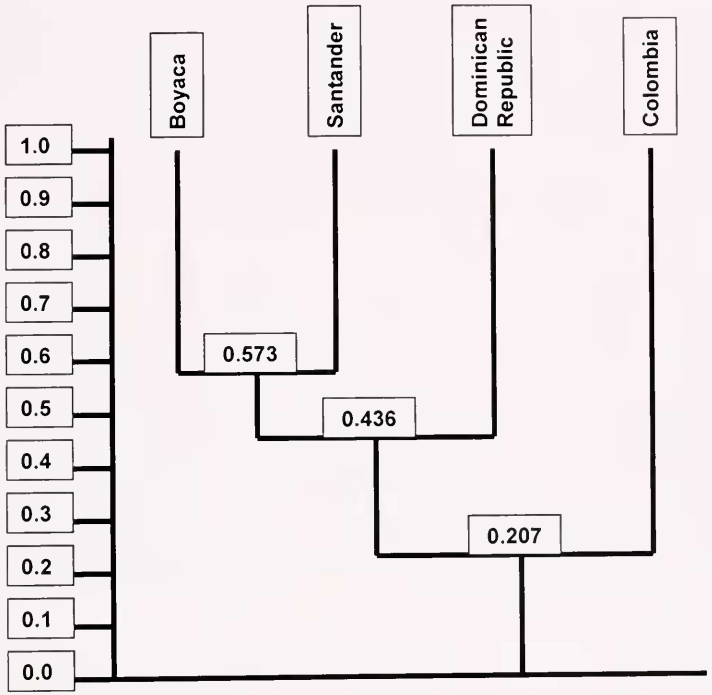

Figure 1. Unweighted pair group cluster analysis of Jaccard's Coefficient of Similarity. Ant faunas preserved in copal from Boyaca Department, Colombia, from Santander Department, Colombia preserved in amber from the Dominican Republic, and existing ant fauna of Colombia are clustered. A coefficient of 1 would indicate complete similarity; a coefficient of 0 would indicate complete dissimilarity. For further discussion, refer to text.

Examination of genera preserved in copal from Boyaca and Santander departments exhibit differences, which may indicate different environments. For example, more genera that typically forage at or near the soil surface are known from Santander copal. *Azteca* species typically nest in trees. Approximately 56% of all specimens from Boyaca are *Azteca* compared to 1% of all specimens from Santander. Both sites trapped comparable numbers of genera (Boyaca with 20 genera and Santander with 23 genera); there are 15 genera in common. Yet, Santander had roughly 30% of all specimens while Boyaca had 70%. Fully 50% of all genera from Santander are myrmicines.

Similarities exist between the faunas. For example, representatives of Attini are found in both deposits (Boyaca has *Acromyrmex* and Santander has *Atta*).

The copal ant faunas from Colombia are more similar to that of the ants found in amber from the Dominican Republic than to the modern Colombian ant fauna (Fig. 1). However, it is presumed the copal material is much younger than the ant material preserved in amber from the Dominican Republic. We suspect the main reason for this similarity is that plant resins trap a subset of the ant fauna in a given area. The fauna of Colombia is much more diverse than could be encountered in a few locations (much larger area with many divergent habitats). It should be significantly different from the fauna obtained in a small area.

Alpha Diversity Measures (Quantitative Data)

These measures attempt to account for richness (number of species) or evenness (equal abundance). It is presumed that material from both sites in Colombia was trapped in a similar manner and that both sites (when fully excavated) are similar in size. Several measures were selected as they have different sensitivity to sample size variation, discriminant ability, and a bias towards richness or evenness. Magurran (1988: 79) discussed details regarding sensitivity and bias of these measures. DuBois (1995) discussed the use of these selected measures in dealing with ant faunas. For each measure, calculations for Boyaca and Santander are listed and compared with calculations for the ant fauna of central North America (DuBois, 1995).

α Measure	Boyaca	Santander	North America
Margaleff's Index	3.49	4.78	13.4
Simpson's Index reciprocal	2.99	8.78	34.0
Shannon's Index	1.75	2.60	3.5
Q-statistic	4.83	10.10	24.6
Berger-Parker Index	0.56	0.26	0.1
Alpha (or log series)	4.91	10.14	25.6
Pielou's Evenness Index	0.60	0.82	0.8

We believe the reason the majority of the above calculations were low for tropical areas is that a limited portion of the total ant fauna was trapped in the resin. Many species forage in a manner that does not lend itself to ready exposure to resin. Also, given that there may have been seasonality to resin flows, reproductives of other species inhabiting the area may not have been trapped.

DISCUSSION

This paper briefly discusses some of the ant diversity found in copal. While these hardened resins are not as old as much other material previously studied, they are worthy of further investigations. For example, even relatively young material provides a clearer picture of the ant fauna prior to intense human activities in South America. For this reason alone, this material is worthy of

further investigation. Once more accurate ages are determined, this material should be re-examined and implications concerning the presence of various species and genera should be evaluated in greater detail.

We believe this is the first time that ecological measures of biodiversity have been applied to fossil ant assemblages. Such measures should help quantify similarities between different locations over time.

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Appendix

The following ant genera are reported from various copal and amber deposits. Additionally, a list of genera presently known from Colombia is presented. Sources are listed in the text. A plus (+) indicates presence of this genus from a given locality; a minus (-) indicates absence from a given locality. Genera followed by an asterisk have many species which are typically arboreal (nesting and foraging) in South America today. The remaining genera are represented by many species which typically nest and forage on (or near) the soil surface.

Genus	Copal from Boyaca Dept.	Copal from Santander Dept.	Recent Ants from Colombia	Amber from Dominican Republic
Acanthognathus	–	–	+	–
Acanthoponera	–	–	+	–
Acanthostichus	–	–	+	–
Acromyrmex	+	–	+	–
Acropyga	–	–	+	–
Adelomyrmex	–	–	+	–
Allomerus	–	–	+	–
Amblyopone	–	–	+	–

Genus	Copal from Boyaca Dept.	Copal from Santander Dept.	Recent Ants from Colombia	Amber from Dominican Republic
Anochetus	–	–	+	+
Aphaenogaster	–	–	+	+
Apterostigma	–	–	+	–
Atta	–	+	+	–
Azteca *	+	+	+	+
Basiceros	–	–	+	–
Belonopelta	–	–	+	–
Blepharidatta	–	–	+	–
Brachymyrmex	–	–	+	–
Camponotus *	+	+	+	+
Carabarella	–	–	+	–
Cardiocondyla	–	–	+	–
Centromyrmex	–	–	+	–
Cephalotes *	+	–	+	–
Cerapachys	–	–	+	–
Cheliomyrmex	–	–	+	–
Creightonidris	–	–	+	–
Crematogaster *	+	+	+	+
Cylindromyrmex	–	–	–	+
Cyphomyrmex	–	–	+	+
Daceton *	–	–	+	–
Dendromyrmex *	–	–	+	–
Dinoponera	–	–	+	–
Discothyrea	–	–	+	–
Dolichoderus *	+	+	+	+
Dorymyrmex	–	–	+	–
Eciton	–	–	+	–
Ectatomma	–	–	+	–
Erebomyrma	–	–	–	+
Eucryptocerus *	–	–	+	–
Eurhopalothrix	–	–	+	–
Forelius	+	+	+	–
Gigantiops	–	–	+	–
Glamyromyrmex	–	–	+	–
Gnamptogenys	+	+	+	+
Heteroponera	–	–	+	–
Hylomyrma	–	–	+	–
Hypoponera	+	+	+	+
Hemomyrmex	–	–	–	+
Labidus	–	–	+	–
Lachnomyrmex	–	–	+	–
Leptanilloides	–	–	+	–
Leptogenys	–	–	+	–
Leptothorax	–	–	+	+
Linepithema	+	+	+	+
Megalomyrmex	–	–	+	–
Monomorium	–	–	+	–

Genus	Copal from Boyaca Dept.	Copal from Santander Dept.	Recent Ants from Colombia	Amber from Dominican Republic
Mycetophylax	–	–	+	–
Mycocepurus	–	–	+	–
Myrmecina	–	+	–	–
Myrmelachista	–	–	+	–
Myrmicocrypta	–	–	+	–
Unidentified Myrmicinae	+	–	–	–
Neivamyrmex	–	+	+	+
Neostruma	–	–	+	–
New genus	–	–	–	+
Nomamyrmex	–	–	+	–
Ochetomyrmex	–	–	+	–
Octostruma	–	–	+	+
Odontomachus	–	+	+	+
Oligomyrmex	–	–	+	–
Oxydris	–	–	–	+
Pachycondyla	+	+	+	+
Paraponera	–	–	+	+
Paratrechina	+	+	+	+
Pheidole	+	+	+	+
Platythyrea	+	+	+	+
Pogonomyrmex	–	–	+	–
Prenolepis	–	–	–	+
Prionopelta	–	–	+	+
Probolomyrmex	–	–	+	–
Proceratium	+	–	+	–
Procryptocerus *	–	–	+	–
Prodimorphomyrmex	–	–	–	+
Protalaridris	–	–	+	–
Pseudomyrmex *	+	+	+	+
Rhopalothrix	–	–	+	–
Rogeria	+	–	+	–
Sericomyrmex	–	–	+	–
Simopelta	–	–	+	–
Smithistruma	–	+	+	+
Solenopsis	+	+	+	+
Stenamma	–	–	+	–
Strumigenys	–	+	+	–
Tapinoma	+	+	+	+
Tetramorium	–	–	+	–
Thaumatomyrmex	–	–	+	–
Trachymyrmex	–	–	+	+
Tranopelta	–	–	+	–
Typhlomyrmex	–	–	+	–
Wasmannia	–	–	+	–
Zacryptocerus *	+	+	+	+